

PHYLOGENETIC POSITION OF *MONONYKUS* (AVES: ALVAREZSAURIDAE) FROM  
THE LATE CRETACEOUS OF THE GOBI DESERT

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In order to assess the phylogenetic relationships of *Mononykus*, a cladistic analysis was performed. Using velociraptorine theropods as outgroups, the analysis resulted in a single most parsimonious cladogram. In this cladogram the monophyletic Alvarezsauridae (including *Mononykus* and the Argentine *Alvarezsaurus* and *Patagonykus*) is the sistergroup of all other birds except *Archaeopteryx*. The monophyly of Aves (= Avialae sensu Gauthier) is supported by seven unambiguous synapomorphies, four of which are present in *Mononykus*. These characters include fewer than 26 caudal vertebrae, caudal vertebrae with short distal prezygapophyses, teeth with unserrated crowns and a caudal tympanic recess opening only inside the tympanic cavity. The monophyly of Metornithes (Aves exclusive of *Archaeopteryx*) is supported by six unambiguous synapomorphies all of which occur in *Mononykus*. Among these characters are the presence of prominent ventral processes on the cervicodorsal vertebrae, a carpometacarpus, a prominent antitrochanter in the pelvis and a rectangular, carinate sternum. Furthermore, six synapomorphies (all present in *Mononykus*) ambiguously diagnose both Aves and Metornithes. The distribution among avian and nonavian taxa of all these characters is discussed. Several authors have criticised the hypothesis of avian relationships for *Mononykus*. In this paper we address those criticisms. We also discuss the rationale of testing phylogenetic hypotheses within a cladistic framework and establish that our critics have not furnished much beyond a priori speculation. □ *Birds, Cretaceous, phylogeny, homology.*

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One of the central problems in palaeontology is the origin of the major groups of terrestrial amniotes. One of these, birds, has received intense scrutiny ever since, and even before, the first specimens of *Archaeopteryx lithographica* were collected. Since the publication of the London specimen in 1861 (Meyer, 1861), this and subsequent specimens of *Archaeopteryx* have been key elements in discussions of bird origins.

Surprisingly, except for specimens of *Hesperornis* and *Ichthyornis*, it took over a hundred years for significant new specimens of basal birds to be recognised (Chiappe, 1995a, b). The last 15 years, however, has seen surprising progress on this front and many important new specimens of basal birds have been described (e.g., Walker, 1981; Kurochkin, 1985; Sanz et al., 1988, 1995; Chiappe, 1991, 1993, 1995a, b; Alvarez & Bonaparte, 1992; Sanz & Buscalioni, 1992; Sereno & Rao, 1992; Wellnhofer, 1992, 1993; Zhou et al., 1992; Chiappe & Calvo, 1994; Hou et al., 1995).

*Mononykus olecranus* (Perle et al., 1993) from the Late Cretaceous of Mongolia, is one of the most unusual of these (Fig. 1). *Mononykus* is larger than most basal birds and instead of well developed wings it possessed stout arms that are ridiculously short, terminating in a robust hand with a hypertrophied digit (Perle et al., 1993, 1994; Norell et al., 1993a). Many other aspects of its morphology are a peculiar melange of primitive, derived and just plain weird (Perle et al., 1994). Apparently, *Mononykus* was a common element of the Late Cretaceous fauna of Central Asia (Norell et al., 1993a). In the last few years many specimens have been collected at several Mongolian localities by the Mongolian American Museum Paleontological Project (Novacek et al., 1994; Dashzeveg et al. 1995). Furthermore, specimens collected during the 1920s from the Djadokhta Formation at Bayn Dzak (Norell et al., 1993a) and the Iren Dabasu Formation in northern China have been recently found in the collections of the AMNH. In earlier papers, we predicted that such a highly recognisable mor-

phology may foster discovery of members of this clade in other faunas, where material is usually more poorly preserved. Recently, close relatives of *Mononykus* have been identified in the Late Cretaceous of Argentine Patagonia (Novas, this volume). Because of this discovery a discussion of the phylogenetic relationships of *Mononykus* fits the scope of a symposium on Gondwanan dinosaurs.

In our 1993 paper we proposed a hypothesis based on shared derived characters placing *Mononykus* in a sister-group relationship to all birds except *Archaeopteryx* (Perle et al., 1993, 1994). The discovery of

*Patagonykus* and the reinterpretation of *Alvarezsaurus* as another relative of *Mononykus* (see Novas, this volume) documented that the Alvarezsauridae (e.g., *Alvarezsaurus*, *Mononykus*, and *Patagonykus*) comprise a diverse, but monophyletic group of primitive birds not only present in the Late Cretaceous of central Asia but also in southern South America and probably in western North America (Holtz, 1994a). In this paper, we summarise the evidence supporting the sister-group relationship of Alvarezsauridae to all other birds except *Archaeopteryx*, making emphasis on *Mononykus* [see Novas (this volume) for information on *Alvarezsaurus* and *Patagonykus*]. Phylogenetic relationships among Alvarezsauridae are discussed elsewhere (see Novas, this volume).

#### MATERIALS AND METHODS

**ANATOMICAL NOMENCLATURE.** Anatomical terms mostly follow Baumel & Witmer (1993), using the English equivalents of the Latin terminology. The extrapolation of modern avian nomenclature to successive sister groups and even non-avian theropods is based on acceptance of the theropod hypothesis of avian origins (Ostrom, 1976a; Gauthier, 1986). For most features of modern birds it is possible to trace homologous structures in more basal birds and non-avian theropods.

**TAXONOMIC NOMENCLATURE.** In recent years there has been disagreement as to what taxa comprise Aves. Traditionally it is used to name a group including all species descended from the last common ancestor of *Archaeopteryx*

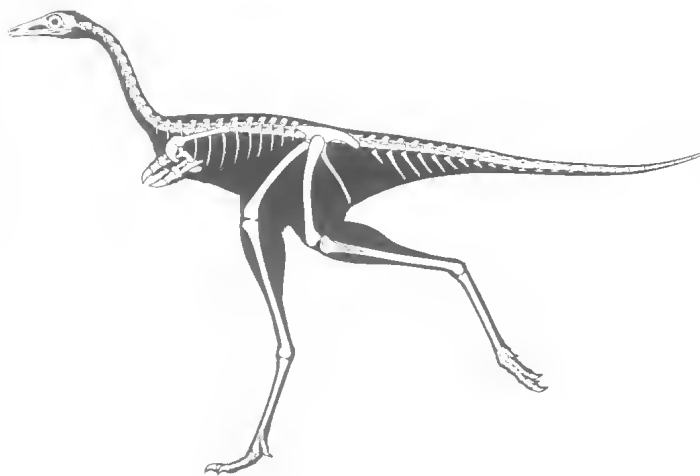


FIG. 1. Skeletal reconstruction of *Mononykus* (modified from Perle et al., 1994).

*lithographica* and modern birds (Neornithes), although Hennig's (1969, 1981) concepts of total group (e.g., Ax, 1987; Patterson, 1993) and crown group (e.g., Gauthier, 1986; Norell et al., 1993b; Perle et al., 1993, 1994) have been also applied to this clade. Using the latter concept, Gauthier (1986) recognised the term Avialae to name the clade traditionally named with the term Aves (see also Rowe & Gauthier, 1992; De Queiroz & Gauthier, 1992). In doing this, Gauthier (1986) replaced the term Neornithes — traditionally used to name this group — by redefining the term Aves. In this paper — based on the preferences of the senior author — we follow the traditional nomenclature and therefore we use the term Aves to name a clade composed of the common ancestor of *Archaeopteryx lithographica* and modern birds (Neornithes) plus all its descendants. Note that this definition uses a node-based phylogenetic definition (see De Queiroz & Gauthier, 1992) and not a character-based — usually feathers — definition of the taxon Aves. Therefore, the inclusion of a particular taxon within Aves is only based on its genealogical history. The collective terms 'modern birds' and 'birds' refer to all members of the monophyletic taxa Neornithes and Aves, respectively, while 'nonavian theropods' refer to all theropod outgroups of birds, used without any implication of monophyly.

**PHYLOGENETIC ANALYSIS.** The character analysis includes 99 characters (Appendix 1). Ten of these are multistate characters. All characters were treated as additive (any two states are

separated by a number of steps that equals their absolute arithmetic difference) except for four multistate characters (34, 40, 64 & 92) that were treated as non-additive (any two states are separated by a single step). The data set was processed using the computer program 'Hennig 86' (Farris, 1988). Using the implicit enumeration (ie) command — which generates trees that are certain to be of minimal length — a single most parsimonious tree was obtained (Fig. 2). In order to address the character optimisation in alternative topologies, the resultant tree was re-rooted by using the dos equis (xx) command of 'Hennig 86' (see Discussion).

Because our objective is to assess relationships rather than diagnose all groups, only characters in which the derived state (or at least one of the derived states of a multistate character) is present in two or more different terminal taxa were analyzed. In order to avoid influence on the consistency index, derived characters exclusive to a single terminal taxon were not included (Carpenter, 1988; Wiley et al., 1991). As the result of the phylogenetic analysis, however, some characters are autapomorphies of different taxa (e.g., characters 64a, 98; Fig. 2).

Polarisation of character states used in the character analysis was established by using velociraptorine theropods as the outgroup. We are aware that the use of a different outgroup (e.g., Troodontidae, Oviraptoridae) might result in a different tree topology. This decision, however, was based on a combination of previous phylogenetic research with the anatomical information currently at hand: Several recent phylogenetic hypotheses on maniraptoran dinosaurs have considered velociraptorine theropods (e.g., *Deinonychus*, *Velociraptor*, *Adasaurus*) as closely related to birds (Gauthier, 1986; Novas, 1992; Holtz, 1994b) and the available information on other nonavian maniraptoran dinosaurs (e.g., troodontids, oviraptorids, segnosaurids) is still limited.

The analysed ingroup included taxa hypothesised to be closely related to *Mononykus* such as the Argentine *Alvarezsaurus* (Bonaparte, 1991) and *Patagonykus* (Novas, this volume), along with the best represented avian taxa: *Archaeopteryx*, *Iberomesornis*, Enantiornithes, *Patagopteryx*, Hesperornithiformes, Ichthyornithiformes and Neornithes.

**MATERIAL EXAMINED.** The anatomical information on Velociraptorinae was based mostly on the AMNH and YPM's specimens of *Deinonychus antirrhopus* (Ostrom, 1969) and the holotype, and several new unpublished specimens (see Norell et al., 1992) of

*Velociraptor mongoliensis* (Osborn, 1924). Additional information was taken from Ostrom (1969, 1974, 1976b, 1990) and Barsbold (1983).

Five specimens of *Mononykus olecranus* were used in this study: the holotype (MGI 107/6) and specimens MGI N100/99, MGI 100/975, MGI 100/977 and IGM 100/1001. The holotype specimens of *Alvarezsaurus calvoi* (Bonaparte, 1991) and *Patagonykus puertai* (Novas, this volume) from the Late Cretaceous of Patagonia (Argentina) were also studied.

The osteological data on *Archaeopteryx lithographica* was taken from De Beer (1954), Wellnhofer (1974, 1992, 1993), Ostrom (1976a), Martin (1983), Whetstone (1983), Walker (1985), Bühler (1985), Witmer (1990) and Elzanowski & Wellnhofer (1995) as well as examination of the Eichstätt, Solnhofen and London specimens, and a cast of the Berlin specimen. The holotype specimen of *Iberomesornis romerali* (Sanz et al., 1988; Sanz & Bonaparte, 1992) was also studied. Almost all the available material of Enantiornithes was examined, including undescribed specimens from the Late Cretaceous of Argentina (El Brete; see Chiappe, 1993, 1996) and specimens of *Enantiornis leali* (Walker, 1981; Chiappe, this volume), *Lectavis brenticola* (Chiappe, 1993), *Yungavolucris brevipedalis* (Chiappe, 1993), *Soroavisaurus australis* (Chiappe, 1993), *Neuquenornis volans* (Chiappe & Calvo, 1994), *Concornis lacustris* (Sanz & Buscalioni, 1992; Sanz et al., 1995) and *Cathayornis yandica* (Zhou et al., 1992). Casts of the enantiornithines *Sinornis santensis* [Serenó & Rao, 1992; arguments supporting its inclusion within Enantiornithes are presented elsewhere (Chiappe, 1995b)], *Avisaurus gloriae* (Varricchio & Chiappe, 1995), *Avisaurus archibaldi* (Brett-Surman & Paul, 1985; Chiappe, 1992b, 1993) and *Nanantius eos* (Molnar, 1986) were also studied. All the available material of *Patagopteryx deferrariisi* (Alvarenga & Bonaparte, 1992; Chiappe, 1992a, 1996) was also examined. The anatomical data on the Hesperornithiformes mostly derives from the seminal monograph of Marsh (1880), and papers of Martin & Tate (1976), Martin (1980, 1983, 1984), Bühler et al. (1988), Witmer (1990) and Elzanowski (1991). Specimens at the AMNH, FMNH, UK and YPM were also examined. Information on Ichthyornithiformes was derived mainly from Marsh's (1880) description of *Ichthyornis dispar* and *Ichthyornis victor* and the study of specimens labeled as *Ichthyornis* sp. at the YPM. The skeletal material of different representatives of several groups of modern paleognathes and neognathes (Aves) was surveyed. This information was supplemented by such general osteological papers such as Jollie (1957), Webb (1957), Bellairs & Jenkin (1960), King & McLelland (1984) and Baumel & Witmer (1993).

**Institutional Abbreviations.** AMNH, American Museum of Natural History (New York); FMNH, Field Museum of Natural History (Chicago); MGI, Mongolian Geological Institute (Ulan

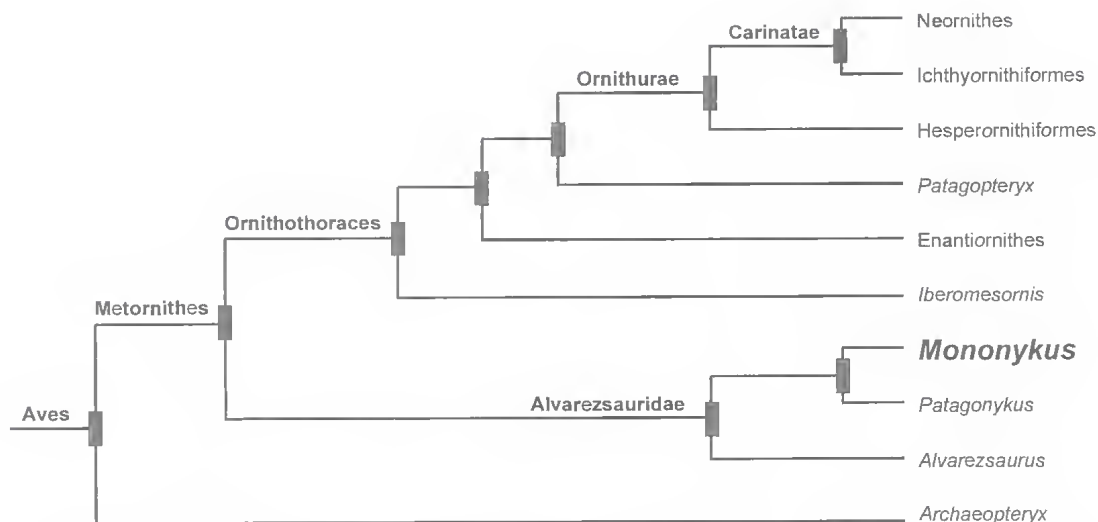


FIG. 2. Analysis cladogram. Coding: asterisked characters (\*) have equivocal optimization; the symbol (-) indicates a character reversal; 'a' and 'b' refer to states 1 and 2, respectively, of a multistate character (see Appendix 1). NODE 1 (Aves = Avialae sensu Gauthier, 1986): 11\*, 15\*, 19a, 23a, 46\*, 59a\*, 68\*, 71, 72\*, 74\*, 81, 83\*, 84\*, 85a, 86\*, 87, 88, 90\*, 95\*, 96\*. NODE 2 (Metornithes): 6\*, 8\*, 11\*, 13, 14a\*, 15\*, 29, 30, 31\*, 34a\*, 34b\*, 36\*, 39, 41\*, 44, 45\*, 46\*, 47\*, 51\*, 55\*, 59a\*, 68\*, 69, 72\*, 74\*, 83\*, 84\*, 86\*, 90\*, 92a\*, 95\*, 96\*. NODE 3 (Ornithothoraces): 1\*, 3\*, 5\*, 6\*, 7\*, 8\*, 10\*, 11\*, 14a\*, 18, 21\*, 23b, 24\*, 25, 26\*, 27, 31\*, 32\*, 34a\*, 34b\*, 36\*, 37\*, 38, 40a\*, 40b\*, 41\*, 45\*, 47\*, 50\*, 51\*, 53\*, 54a\*, 55\*, 60\*, 63\*, 67\*, 70\*, 72\*, 83\*, 84\*, 86\*, 90\*, 92a\*, 93\*, 96\*, 97\*. NODE 4: 1\*, 3\*, 5\*, 6\*, 7\*, 10\*, 11\*, 16, 17, 19b\*, 21\*, 24\*, 26\*, 31\*, 32\*, 34b\*, 35, 36\*, 37\*, 40a\*, 40b\*, 45\*, 47\*, 50\*, 51\*, 53\*, 54a\*, 55\*, 56, 60\*, 62, 63\*, 67\*, 70\*, 72\*, 73, 76\*, 83\*, 84\*, 86\*, 90\*, 92a\*, 93\*, 96\*, 97\*. NODE 5: 2\*, 4\*, 6\*, 7\*, 10\*, 11\*, 19b\*, 28, 31\*, 32\*, 40a\*, 40b\*, 45\*, 47\*, 49, 54b, 55\*, 61, 66, 67\*, 70\*, 72\*, 76\*, 82, 85b, 87\*, 90\*, 92a\*, 93\*, 94\*, 97\*. NODE 6 (Ornithurae): 2\*, 4\*, 6\*, 7\*, 9, 11\*, 12, 14b, 19b\*, 20, 22, 32\*, 40a\*, 40b\*, 42, 43, 48, 52, 57, 58, 59b, 64b, 65, 67\*, 70\*, 72\*, 87\*, 91\*, 92a\*, 93\*, 94\*, 97\*, 99\*. NODE 7 (Carinatae): 11\*, 32?, 33, 40b\*, 70\*, 87\*, 91\*, 92a\*, 92b\*, 99\*. NODE 8 (Alvarezsauridae, see Novas, this volume): 6\*, 8\*, 11\*, 14a\*, 23\*, 31\*, 34a\*, 34b\*, 36\*, 41\*, 45\*, 47\*, 48\*, 51\*, 55\*, 75\*, 78\*, 79\*, 80\*, 83\*, 84\*, 89, 90\*, 92a\*, 96\*. NODE 9: 6\*, 8\*, 11\*, 14a\*, 23\*, 31\*, 34a\*, 36\*, 41\*, 47\*, 48\*, 51\*, 75\*, 76, 77, 78\*, 79\*, 80\*, 83\*, 84\*, 90\*, 92a\*, 96\*. Resultant apomorphies: *Mononykus* (64a), Enantiornithes (98), Neornithes (98). In nodes 4 and 5, if character 76 is synapomorphic, it becomes a reversal in node 6 (Ornithurae).

Bator); UK, Museum of Natural History, University of Kansas (Lawrence); YPM, Yale Peabody Museum (New Haven).

#### CHARACTER ANALYSIS

This analysis resulted in a single most parsimonious cladogram with low homoplasy (length, 143; rescaled consistency index, 0.76; retention index, 0.81). In this cladogram (Fig. 2) the monophyly of Alvarezsauridae (*Mononykus*, *Patagonykus* and *Alvarezsaurus*; see Novas, this volume) is supported, and this group is the sister-group of all birds other than *Archaeopteryx*. In an earlier paper we coined the term 'Metornithes' to name this monophyletic group (Perle et al., 1993).

Below we describe those characters synapomorphic of both Aves and Metornithes and

which are known to be present in *Mononykus*. Reference is made to the condition in the ingroup and outgroup taxa, along with that found in other nonavian theropods. Missing entries are in most cases not mentioned (see data matrix in Appendix 1 for character scoring).

**CHARACTERS SUPPORTING THE MONOPHYLY OF AVES.** The monophyly of Aves (= Avialae sensu Gauthier, 1986) is supported by seven unambiguous synapomorphies (Fig. 2). Four of these (character states 19a, 71, 81 & 85a) are present in *Mononykus*. The available material of *Mononykus* and the remaining Alvarezsauridae does not allow determination of the condition in two of these characters (87 & 88), while *Mononykus* shows the primitive condition for the remaining character (23a). The four avian synapomorphies present in *Mononykus* are:

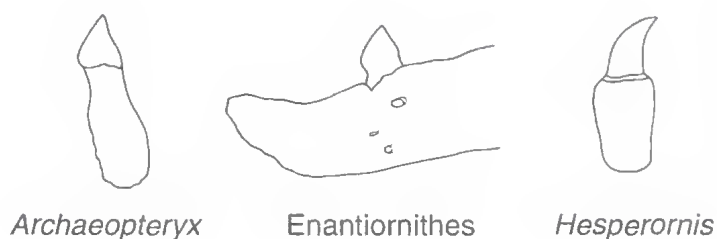


FIG. 3. Avian dental morphology of *Archaeopteryx*, the enantiornithine *Cathayornis* and *Hesperornis*. Drawings not to scale.

1) Caudal vertebral count smaller than 25-26 elements (character 19). In modern birds, the tail is composed of a series of free caudal vertebrae and the pygostyle. The free vertebral count of modern birds ranges between four and eight, being typically between five and seven (Verheyen, 1960). The pygostyle is usually composed of five or six vertebrae (Baumel & Witmer, 1993). Hence, the total caudal count of modern birds (free caudals + pygostyle) includes fewer than 15 elements. Among hesperornithiforms, Marsh (1880) estimated 12 elements in the tail of *Hesperornis* and Martin & Tate (1976) illustrated 14 caudal vertebrae in *Baptornis*. *Iberomesornis* has eight free caudals and a large pygostyle. Some of the elements forming the pygostyle of *Iberomesornis* are clearly distinguishable. Sanz & Bonaparte (1992) correctly estimated that 10 to 15 elements form the pygostyle. Therefore, *Iberomesornis* has a caudal count of no more than 23 vertebrae. In *Archaeopteryx*, the number of caudal elements ranges from 20 to 23 in the different specimens (Ostrom, 1976a).

Velociraptorines and other nonavian theropods, on the contrary, have much longer tails with at least 36 vertebrae (Osborn, 1916; Lambe, 1917; Osmolska et al., 1972; Madsen, 1976). There are approximately 36 to 40 caudal vertebrae in *Deinonychus* (Ostrom, 1969). Curiously, the troodontid *Sinornithoides* (Russell & Dong, 1993a) has 27 preserved caudals and, as estimated by these authors, a total caudal count of no more than 30 elements.

The number of caudal vertebrae in *Mononykus* is significantly lower than in the outgroup and similar to the number found in *Archaeopteryx*. In specimens MGI N100/99 and MGI 100/975, 19 caudal elements are preserved. Some distal elements are missing but based on the size and morphology of the last preserved elements we are

confident in our estimate that the number of caudal elements of *Mononykus* was not larger than 25-26.

2) Teeth with unserrated crowns (character 71). Neornithine birds lack teeth, but a variety of basal birds bear both cranial and mandibular dentition. In the teeth of Hesperornithiformes, Ichthyornithiformes and *Archaeopteryx* the enamel of the crowns is smooth, lacking serrations (Martin et al., 1980; Martin, 1985) (Fig. 3). The same condition is present in the Early

Cretaceous enantiornithine *Cathayornis* (Zhou et al., 1992).

In contrast, adult velociraptorine theropods have serrated crowns (Osborn, 1924; Ostrom, 1969; Currie et al., 1990) (Fig. 4). This is the case for most other non-avian theropods in which the enamel is serrated in at least some areas of the crown tooth (Currie et al., 1990; Fiorillo & Currie, 1994; see Ostrom, 1991 for a few exceptions). In the description of *Archaeornithoides*, Elzanowski & Wellnhofer (1992) considered the absence of dental serrations as a synapomorphy of the clade formed by the latter taxon and birds. The only, and very fragmentary, specimen of *Archaeornithoides* is clearly a juvenile and therefore not an adequate specimen for phylogenetic inferences. As we have recently shown, dromaeosaurid neonates lack serrations as well (Norell et al., 1994), suggesting that in dromaeosaurids, teeth became serrated during postnatal ontogeny. A similar ontogenetic modification is known to occur in extant non-avian archosaurs (i.e., crocodiles). The absence of dental serrations in the juveniles of theropods closely related to birds might indicate that the avian tooth morphology arose through heterochrony (Norell et al., 1994).

In our preliminary description of *Mononykus* (Perle et al., 1993) and in a later paper (Perle et al., 1994), we described a tooth that was found isolated inside the fragmentary skull. The crown of this tooth possesses rostral and caudal carinae and lacks serrations (Fig. 5). Confirmation of this dental morphology has come from a recently discovered articulated specimen (MGI 100/977), including the skull, from the Djadokhta-like red beds of Ukhaa Tolgod (Dashzeveg et al., 1995), in the southwestern Mongol Gobi. In specimen MGI 100/977 both cranial and mandibular teeth



FIG. 4. Teeth of *Velociraptor* (AMNH6518). Note the serrated margins.



FIG. 5. Electron micrograph of a tooth of *Mononykus* (MGI 107/6). Note the complete absence of serrations.

are preserved in their natural position, and they lack serrations.

3) Caudal tympanic recess opens inside the collumelar recess and not in the paroccipital process (character 81). The caudal tympanic recess of modern neornithine birds, the recess formed by the caudal evagination of the tympanic air sac (Witmer, 1990), consistently opens inside the collumelar recess (Witmer, 1990; Baumel & Witmer, 1993). A similar configuration of the tympanic region occurs in Hesperornithiformes and *Archaeopteryx* (Witmer, 1990) (Fig. 6).

The caudal tympanic recess is well-preserved in a recently discovered braincase of *Velociraptor* (Norell et al., 1992). CAT scan imaging has shown that, as in modern birds, it extends inside the paroccipital process. An important difference with birds (Witmer, pers. comm.), however, is that the caudal tympanic recess opens on the rostral surface of the paroccipital process, outside the collumelar recess. This braincase configuration is known to occur in several non-avian theropods such as *Dromaeosaurus* and *Itemirus* (Currie, 1995), *Struthiomimus* and a new maniraptoran from the St Mary River Formation (Witmer & Weishampel, 1993; Witmer, pers. comm.) and *Protoavis* (Chatterjee, 1991), which we do not regard as a bird (see Chiappe, 1995b). Interestingly, Currie & Zhao (1993b) have mentioned that this external paroccipital opening is absent in troodontids.

The tympanic region of *Mononykus* resembles that of *Archaeopteryx*, *Hesperornis* and neor-

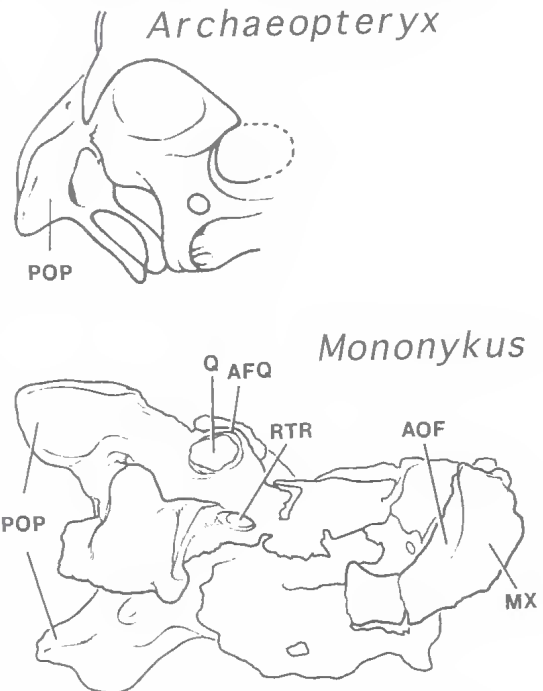


FIG. 6. Braincase morphology of *Archaeopteryx* (redrawn from Walker, 1985) and *Mononykus* (MGI 107/6). Note that the caudal tympanic recess does not open into the paroccipital process. AFQ=articular facet for the quadrate, AOF=antorbital fossa, MX=maxilla, POP=paroccipital process, Q=quadrate, RTR=rostral tympanic recess. Drawings not to scale.

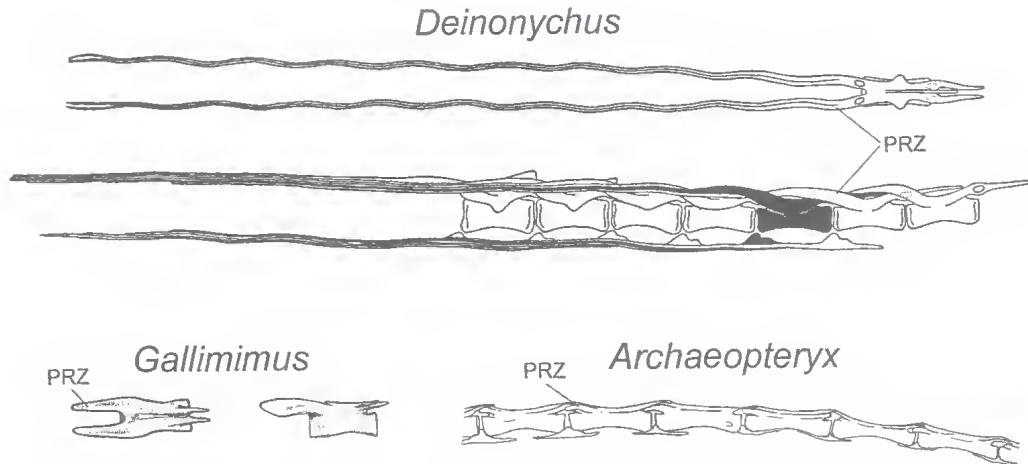


FIG. 7. Caudal vertebrae of *Deinonychus* (after Ostrom, 1969) and *Gallimimus* (twenty second caudal; after Barsbold & Osmólska, 1990) in dorsal and lateral views. Caudal vertebrae of *Archaeopteryx* (tenth to fifteenth vertebrae; after Wellnhofer, 1974). PRZ=prezygapophysis. Drawings not to scale.

nithine birds. In the braincase preserved in the holotype specimen (Perle et al., 1994), the paroccipital process is not perforated by any foramen (Fig. 6) and the caudal tympanic recess opens in the collumelar recess (as in *Archaeopteryx*; contra Currie, 1995).

4) Short or reduced prezygapophyses in distal caudal vertebrae (character 85). The caudal vertebrae of modern birds typically have small, or even absent, prezygapophyses. Caudal prezygapophyses are absent in Hesperornithiformes (Marsh, 1880; Martin & Tate, 1976) and *Patagopteryx* (Chiappe, 1992a). In Ichthyornithiformes (Marsh, 1880), distinct but short prezygapophyses are present in the proximal caudals. Within the Enantiornithes, this character is not determinable in the caudal vertebrae of either *Concornis* (Sanz et al., 1995) or *Cathayornis* (Zhou et al., 1992). Nevertheless, a caudal vertebra preserved in an as yet undescribed enantiornithine specimen from Alabama (Lamb et al., 1993) has short prezygapophyses. The free caudal vertebrae of *Iberomesornis* (Sanz & Bonaparte, 1992) also bear short or reduced prezygapophyses as well. In *Archaeopteryx*, the caudal prezygapophyses appear to be fairly short, extending only slightly over the preceding vertebra (Fig. 7). This is the condition present in the Eichstätt specimen (Wellnhofer, 1974). In the London specimen, the prezygapophyses seem to be longer, however it is hard to provide an accurate estimate of their cranial projection because the articulations between the centra are not ex-

posed. In any case, it is clear that the prezygapophyses of the London specimen are far shorter than those of several non-avian theropods (see below), projecting less than 25% the length of the preceding vertebra.

The presence of remarkably long, rod-like prezygapophyses in the caudal series of velociraptorine theropods is well known (Ostrom, 1969, 1990) (Fig. 7). In *Deinonychus*, the elongate prezygapophyses are present in all caudals distal to the eighth or ninth element (Ostrom, 1969). Elongated prezygapophyses — yet not to extent of the extremely apomorphic condition seen in velociraptorines — are known to occur in the distal caudals of several non-avian theropods, in particular in the middle and distal portions of the tail (see Lambe, 1917; Ostrom, 1969; Barsbold, 1974). The ornithomimid *Gallimimus*, for example (Fig. 7), has distal caudal prezygapophyses extending up to two-thirds the length of the preceding vertebra (Barsbold & Osmólska, 1990) and in *Allosaurus* they extend for at least half the length of the preceding element (Madsen, 1976).

In *Mononykus*, the caudal prezygapophyses, and in particular those of the distal portion of the tail, are short and do not extend to the preceding vertebra. Interestingly, in contrast to those non-avian theropods with long caudal prezygapophyses, the proximal caudal vertebrae of *Mononykus* have prezygapophyses that are longer — though still relatively short — than those of the distal vertebrae (Fig. 8).

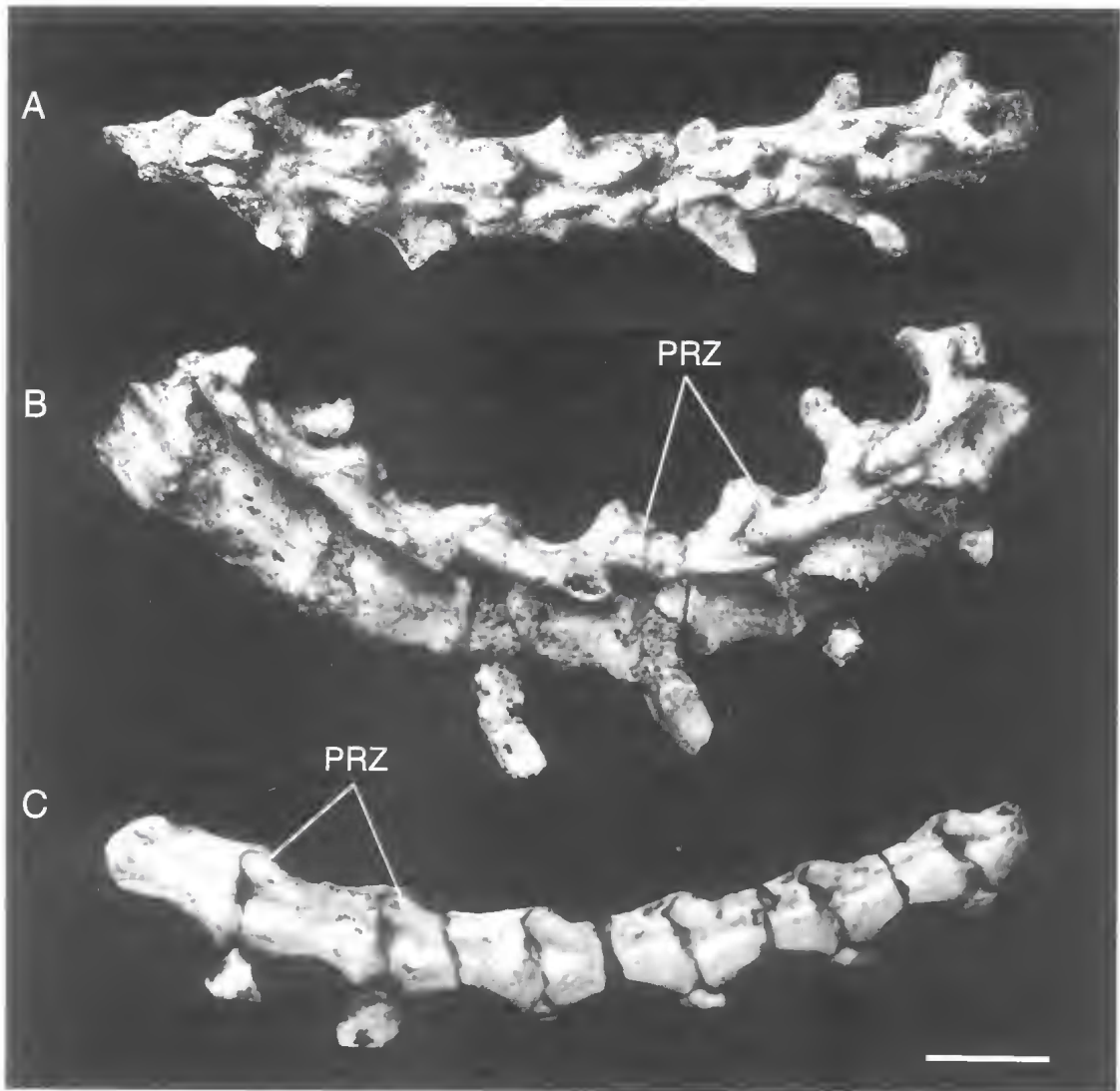


FIG. 8. Caudal vertebrae of *Mononykus* (MGI 100/975). A, B, first? to seventh? vertebrae in dorsal and lateral view. C, 13th? to 19th? vertebrae in lateral view. Note the short prezygapophyses (PRZ). Scale = 1cm.

**CHARACTERS SUPPORTING THE MONOPHYLY OF METORNITHES.** The monophyly of Metornithes (Perle et al., 1993), the clade composed of the closest common ancestor of *Mononykus* and Neornithes plus all its descendants, is supported by six unambiguous synapomorphies. All these synapomorphies are present in *Mononykus*. These synapomorphies are:

1) Prominent ventral processes on cervicodorsal vertebrae (character 13.). The cervicodorsal vertebrae of ornithurine birds (Neornithes,

Hesperornithiformes and Ichthyornithiformes) bear prominent ventral processes for the origin of *M. longus colli ventralis* (Chiappe, 1992a, 1996), a primary depressor of the neck (Zusi, 1962) (Fig. 9). These processes are also well developed in the cervicodorsal vertebrae of *Iberomesornis*, *Enantiornithes* and *Patagopteryx deferrariisi*, but they appear to be absent in *Archaeopteryx* (Chiappe, 1996).

In contrast, ventral processes are only slightly developed in velociraptorine theropods (Ostrom, 1969; Gauthier, 1986) (Fig. 9) and are usually



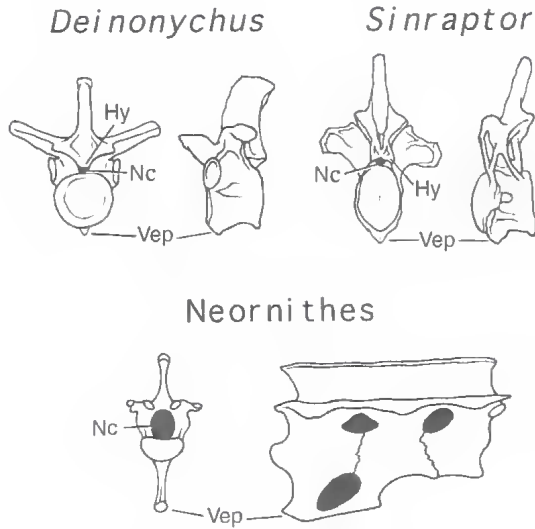


FIG. 9. Dorsal vertebrae of *Deinonychus* (fourth? dorsal; after Ostrom, 1969) and *Sinraptor* (first dorsal; after Currie & Zhao, 1993a) in caudal and lateral views. Dorsal vertebrae of a neornithine bird in cranial and lateral views. Note the large neural canal and the absence of hypantrum in neornithine birds. Hy=hyposphene, Nc=neural canal, Vep=ventral process. Drawings not to scale.

absent (Osborn, 1916; Lambe, 1917; Madsen, 1976; Ostrom, 1978; Bonaparte et al., 1990) or barely developed (Russell & Dong, 1993a; Currie & Zhao, 1993a) in other non-avian theropods (Fig. 9).

In *Mononykus* ventral processes are present in the cervicodorsal region (Fig. 10). In the holotype specimen (Perle et al., 1994), the last two transitional vertebrae between cervicals and dorsals have small ventral processes but the first preserved dorsal bears a much more prominent, well-developed process (Fig. 10). The development of the ventral process of the first(?) dorsal of *Mononykus* resembles that of more advanced birds and not the blunt process of velociraptorine theropods.

2) Sternum of longitudinal rectangular shape (character 29). In the Ornithurae the sternum is typically large and rectangular, with its craniocaudal axis longer than the transverse axis. In these birds, the ratio between maximum length and maximum width (including lateral trabeculae) (ML/MW) is usually larger than 1.4 (Chiappe, 1996). (In some birds with broad sterna, such as Cuculidae, Caprimulgidae, Picidae and Trogonidae, this ratio is slightly smaller). This derived condition is also present in the Enan-

tiornithes. The sterna of the enantiornithines *Neuquenornis* (Chiappe & Calvo, 1994) and *Concornis* (Sanz et al., 1995) are large and rectangular, with a ML/MW ratio of at least 1.66 in the former taxon. In *Archaeopteryx*, in contrast, the sternum is transversely broader than long as has been recently described by Wellnhofer (1993) in the 'Solenhofer Aktien-Verein' specimen (Fig. 11).

In velociraptorines and other non-avian theropods in which sternal ossifications are known, these are formed by two quadrangular plates, which sometimes fuse to each other (Lambe, 1917; Barsbold, 1983; Bonaparte et al., 1990; Currie & Zhao, 1993a). Currie & Zhao (1993a) considered the absence of fusion between sternal plates as related to immaturity. In *Velociraptor* (Fig. 11), the ML/MW ratio is about 1.04 (Barsbold, 1983) and approximately 0.95 and 0.77 in the oviraptorids *Oviraptor* and *Ingenia*, respectively (Barsbold, 1983).

*Mononykus* has a longitudinally rectangular sternum (Perle et al., 1993, 1994), as it has been described in the holotype specimen and corroborated by specimen MGI 100/977 in which the sternum is preserved in natural position. The ML/MW ratio of the sternum of the holotype specimen of *Mononykus* is at least 1.93 (Fig. 12).

3) Ossified sternal keel (character 30). In neornithine birds generally (except in ratites and some other flightless birds), the sternum has a large ventral keel from which the main flight muscles arise. A sternal carina is also present in ichthyornithiforms (Marsh, 1880), in the enantiornithines *Neuquenornis* (Chiappe & Calvo, 1994), *Concornis* (Sanz et al., 1995), and *Cathayornis* (Zhou et al., 1992), but it is absent in hesperornithiforms (Marsh, 1880) and *Archaeopteryx* (Wellnhofer, 1993) (Fig. 11).

In velociraptorines (Fig. 11) and most non-avian theropods in which sternal ossifications are known, the carina is completely absent (Lambe, 1917; Barsbold, 1983; Bonaparte et al., 1990). An exception has been recently reported by Currie & Zhao (1993a) who described a low, blunt ventral keel in the sternum of *Sinraptor*, a taxon related to *Allosaurus*.

In *Mononykus* the sternum has a well-developed ventral keel (Fig. 12). Although carinate, this sternum differs from all other carinate sterna in that it is subtriangular in cross-section and not T-shaped. This latter condition has been considered an apomorphy of *Mononykus* (Perle et al., 1994).

4) Distal carpals fused to metacarpals forming a carpometacarpus (character 39). Neornithine

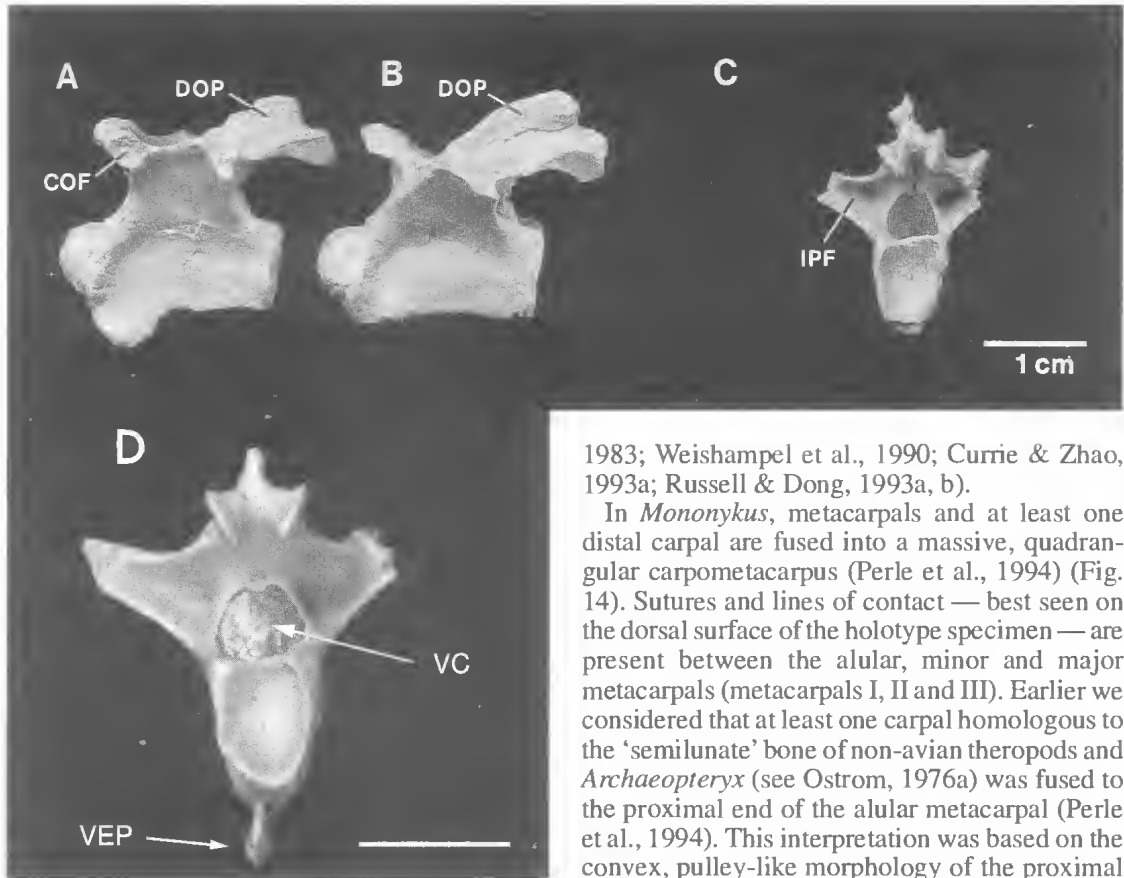


FIG. 10. Dorsal vertebrae of *Mononykus* (MGI 107/6). A, D, anterior first preserved vertebra in lateral and caudal view; B, C, anterior second preserved vertebra in lateral and caudal view. COF=costal fovea (parapophysis), DOP=dorsal process, IPF=infrapostzygapophysial fossa, VC=vertebral canal, VEP=ventral process. Scale = 1cm.

birds have a carpometacarpus formed by the fusion of several central and distal carpals with the metacarpals of the alular, major and minor digits (digits I, II, III) (Fig. 13). Fusion of carpal and metacarpal bones to form a carpometacarpus also occurs in ichthyornithiforms, enantiornithines and *Patagopteryx* (Chiappe, 1996). In contrast a carpometacarpus does not occur in *Archaeopteryx* (Fig. 13), in which the metacarpals fuse neither with each other nor with the distal carpals (Ostrom, 1976a).

The carpals and metacarpals of velociraptorine theropods are not fused to each other (Ostrom, 1969, 1990) (Fig. 13), a condition common to all non-avian theropods (Madsen, 1976; Barsbold,

1983; Weishampel et al., 1990; Currie & Zhao, 1993a; Russell & Dong, 1993a, b).

In *Mononykus*, metacarpals and at least one distal carpal are fused into a massive, quadrangular carpometacarpus (Perle et al., 1994) (Fig. 14). Sutures and lines of contact — best seen on the dorsal surface of the holotype specimen — are present between the alular, minor and major metacarpals (metacarpals I, II and III). Earlier we considered that at least one carpal homologous to the 'semilunate' bone of non-avian theropods and *Archaeopteryx* (see Ostrom, 1976a) was fused to the proximal end of the alular metacarpal (Perle et al., 1994). This interpretation was based on the convex, pulley-like morphology of the proximal end of the carpometacarpus (Fig. 14) which resembles the condition in *Archaeopteryx* and non-avian maniraptoran dinosaurs. Were the 'semilunate' carpal not fused to the alular metacarpal, the proximal end of the latter would be nearly flat to slightly concave, as in non-avian theropods.

#### *Velociraptor*      *Archaeopteryx*

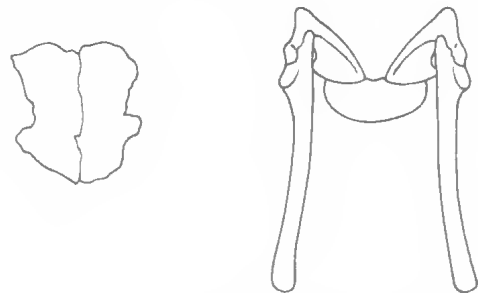


FIG. 11. Sterna of *Velociraptor* (after Barsbold, 1983) and *Archaeopteryx* (after Wellnhofer, 1993) in ventral view. Drawings not to scale.

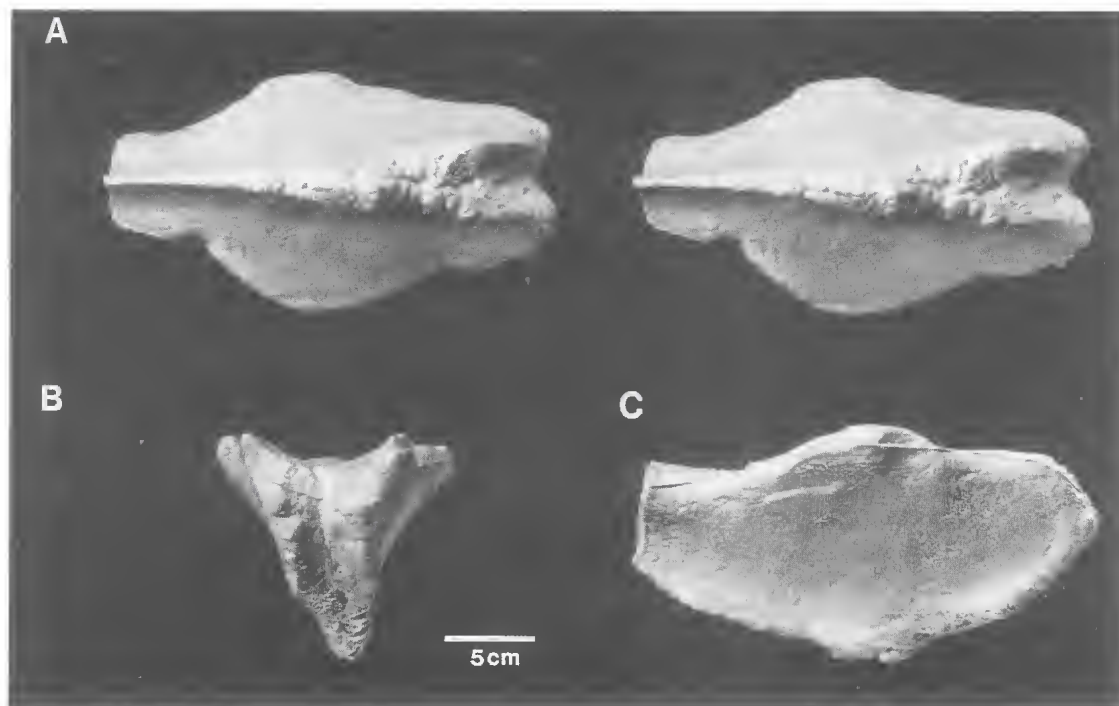


FIG. 12. Sternum of *Mononykus* (MGI 107/6). A, stereopair in ventral view; B, cranial view; C, lateral view.

5) Pelvis with prominent antitrochanter (character 44, Appendix 1). In the caudodorsal angle of the acetabulum of ornithurine birds there is a prominent articular facet, the antitrochanter, typically formed by contributions of the ischium and ilium (Fig. 15). A prominent antitrochanter is found in both *Enantiornithes* and *Patagopteryx* but it is absent in *Archaeopteryx* (Chiappe, 1996) (Fig. 15).

In contrast, a prominent antitrochanter is not developed in velociraptorine theropods (Ostrom, 1969, 1976b) (Fig. 15) nor in any other non-avian theropod (see Osborn, 1916; Osmólska et al., 1972; Madsen, 1976; Weishampel et al., 1990; Currie & Zhao, 1993a; Zhao & Currie, 1993). Russell & Dong (1993a) reported the presence of an antitrochanter in the troodontid *Sinornithoides*, but the absence of detailed illustrations along with the fact that we have not seen the specimen prevents comparisons with those of birds.

In *Mononykus*, the pelvis has a very robust and well-developed antitrochanter (Perle et al., 1994) (Fig. 16). The degree in which both ischium and ilium contribute to the formation of the antitrochanter of *Mononykus* is obscured by the fact that in adult specimens such as the holotype, the ischium and ilium are fused. The fact that the

robust antitrochanter of *Patagonykus* (Novas, this volume) is formed by equal contributions of both ilium and ischium suggests that this was probably the case for *Mononykus*. In contrast to most ornithurine and enantiornithine birds the antitrochanter is developed below the dorsal margin of the acetabulum, and its main axis is not oriented dorsocaudally but caudoventrally (Figs 15, 16). A similar position and orientation of the antitrochanter, however, is present in *Patagopteryx* (Chiappe, 1992a, 1996).

6) Ischium more than two-thirds of pubic length (character 69). In neornithine birds the pubis is longer than the ischium but this difference is typically much less than one-third the length of the ischium (Fig. 15). The pubis is only slightly longer than the ischium in hesperornithiforms, *Patagopteryx* (Fig. 15) and the enantiornithines *Concornis* (Sanz et al., 1995) and *Sinornis* (Serenó & Rao, 1992). In contrast, in *Archaeopteryx* the length of the ischium is between 44 to 48% that of the pubis (Wellnhofer, 1985, 1992) (Fig. 15). Interestingly, the ischium appears to be proportionally shorter in the 'Solenhofer Aktien-Verein' specimen, recognised as a different species — *Archaeopteryx bavarica* instead of *Archaeopteryx lithographica* — by Wellnhofer (1993).

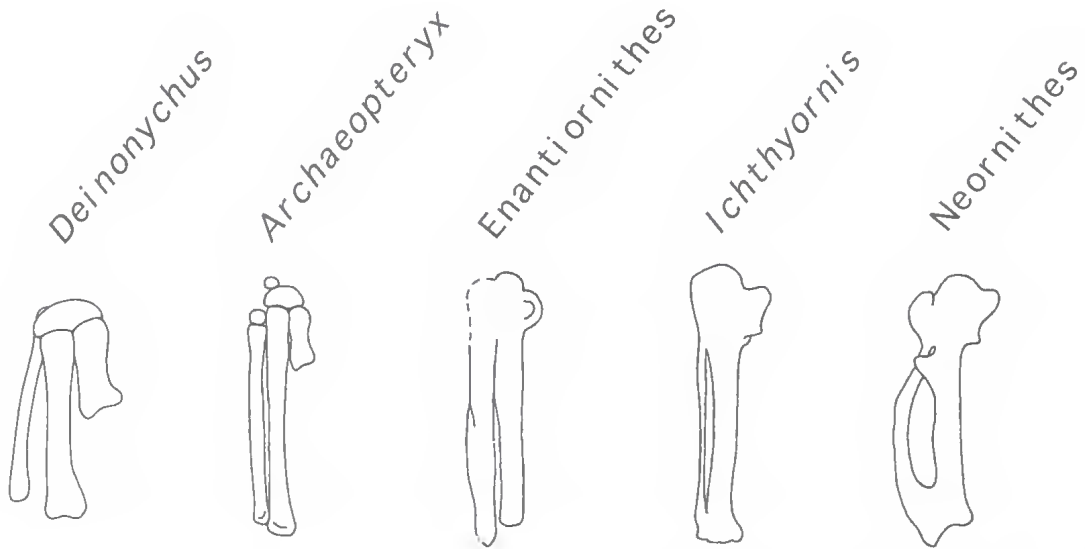


FIG. 13. Distal carpals and metacarpals of *Deinonychus*, *Archaeopteryx*, *Enantiornithes*, *Ichthyornis* and *Neornithes*. Note the fusion of these elements in the three latter taxa.

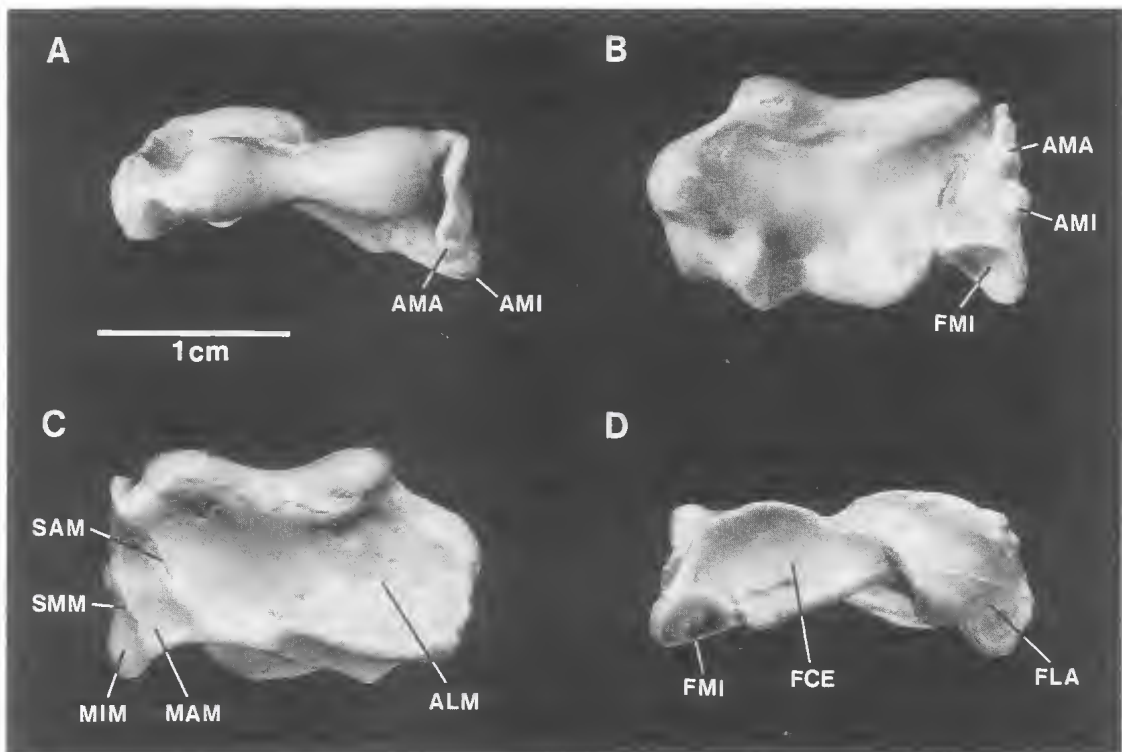


FIG. 14. Carpometacarpus of *Mononykus* (MGI 106/7). A, distal view; B, ventral view; C, dorsal view; D, proximal view. ALM=alular metacarpal, AMA=articular facet of major metacarpal, AMI=articular facet of minor metacarpal, FCE=central proximal articular facet, FLA=lateral proximal articular facet, FMI=proximal articular facet of minor metacarpal, MAM=major metacarpal, MIM=minor metacarpal, SAM=suture between alular and major metacarpals, SMM=suture between major and minor metacarpals.

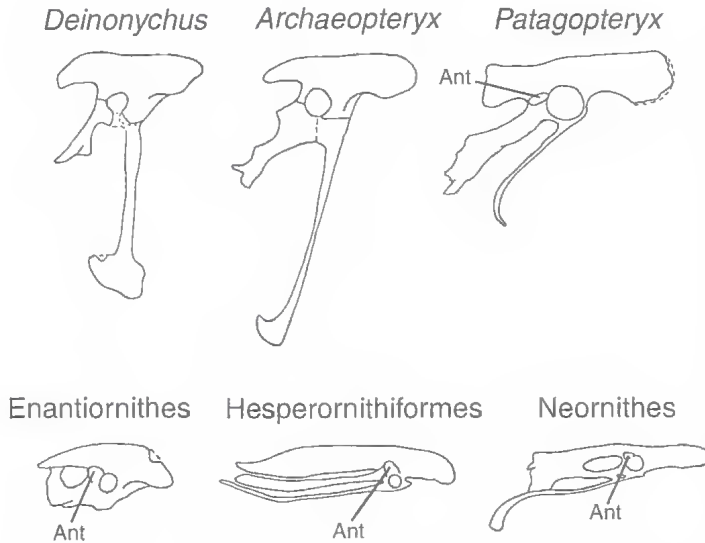


FIG. 15. Lateral view of the pelvis of *Deinonychus*, *Archaeopteryx*, *Patagopteryx*, *Enantiornithes*, *Hesperornithiformes* and *Neornithes*. Ant=antitrochanter. Drawings not to scale.

Velociraptorine theropods, as in other non-avian maniraptoran theropods (e.g., Russell & Dong, 1993a), have ischia that are two-thirds or less the length of the pubis (Gauthier, 1986). In *Deinonychus* (Ostrom, 1976b) and *Adasaurus* (Barsbold, 1983), the ischium is nearly 50% the size of the pubis (Fig. 15). In contrast, in *Mononykus*, both pubis and ischium — oriented some 45° caudoventrally — have delicate, rod-like shafts of subequal length (Fig. 17).

Gauthier (1986) has hypothesised that the more similar length of the pubis and ischium in ornithurine birds was acquired through reduction of the former bone. Nevertheless, the fact that the obturator process of the ischium of these birds is located proximally and not mediodistally as in velociraptorines or *Archaeopteryx* suggests the opposite. It is probably the elongation of the ischiadic blade that accounts for the proportion seen in ornithurine birds.

**AMBIGUOUS SYNAPOMORPHIES EXCLUSIVE OF BOTH AVES AND METORNITHES.** Additional support for the avian affinity of *Mononykus* and the Alvarezsauridae comes from six other characters in which optimisation is ambiguous or equivocal for the present character distribution. A closer examination of the data indicates that the ambiguity for this optimisation is mostly derived from the fact that these character states are uncertain in *Archaeopteryx*. It is

important to note that given a known morphology for *Archaeopteryx*, these characters would be unambiguously synapomorphic of either Aves or Metornithes. The fact that these character states are clearly not present in the outgroup, and that they represent symplesiomorphies for clades more derived than Alvarezsauridae, provides further support for our hypothesis. These synapomorphies are:

1) Wide vertebral foramen in dorsal vertebrae, vertebral foramen/cranial articular facet ratio greater than 0.40 (character 15). The dorsal vertebrae of modern, neornithine birds possess a large vertebral foramen (Chiappe, 1996) (Fig. 9). Despite wide variation, in the sample of neornithine birds taken for this study, the ratio between the vertical diameters of the vertebral foramen and the cranial articular surface ranges approximately from 0.55-2.75. Typically, the anterior dorsals give larger ratios than the posterior ones. In hesperornithiforms and ichthyornithiforms this value is at least 0.70 (Marsh, 1880). In *Enantiornithes* and *Patagopteryx*, although the size of the vertebral foramen falls among the lower values observed in neornithine birds, the ratio is clearly greater than 0.40.

A quite contrasting condition occurs in velociraptorines and other non-avian theropods in which the vertebral foramen of the dorsal vertebrae is very small (Fig. 9), with the above ratio being much lower than 0.40 (see for example Ostrom, 1969; Madsen, 1976; Currie & Zhao, 1993a). In the holotype specimen of *Mononykus*, however, the ratio between the vertebral foramen/articular cranial facet is approximately 0.75 in the anterior-most dorsals (Fig. 10) and about 0.58 in the more posterior biconvex vertebra. This ratio is approximately 0.45 in the only dorsal vertebra of *Patagonykus* that preserves the cranial portion (Novas, this volume, in press).

2) Lack of contact between ischial terminal processes (lack of ischial symphysis) (character 46). In all ornithurine birds, excepting only the Rheidae (i.e., rheas), the terminal processes of the ischia do not contact with each other. The ischiadic terminal processes do not contact each other in *Enantiornithes* (based on *Concornis*; see

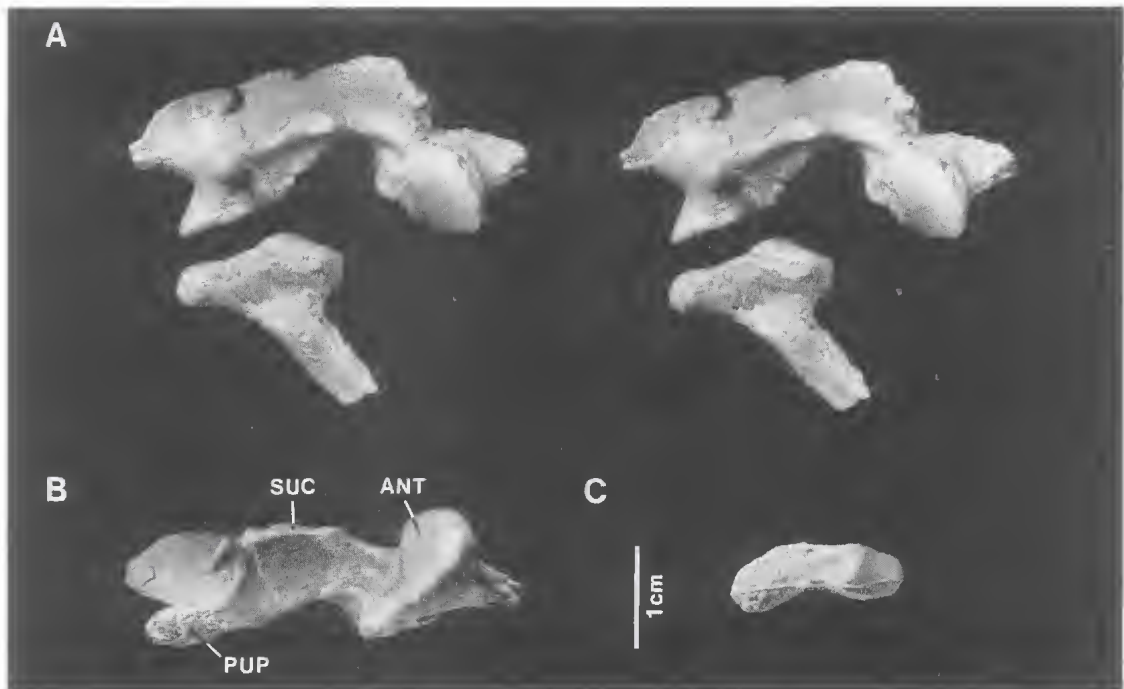


FIG. 16. Pelvis of *Mononykus* (MGI 106/7). A, stereopair of lateral view of the ilium and pubis; B, ventral view of the ilium; C, proximal view of the pubis. ANT=antitrochanter, PUP=pubic peduncle, SUC=supraacetabular crest.

Sanz et al., 1995) and *Patagopteryx* (Chiappe, 1992a, 1996).

In velociraptorines and the remaining non-avian theropods (Romer, 1956; Osmólska et al., 1972; Madsen, 1976; Currie & Zhao, 1993a) the ischia form a terminal symphysis. In contrast, in *Mononykus* the distal ends of the ischia do not contact each other (Perle et al., 1993, 1994), as is clearly visible in specimens MGI N 100/99 and MGI 100/975 in which the pelvic elements are in articulation.

3) Fibular tubercle for *M. iliofibularis* laterally projecting (character 59, Appendix 1). In the fibula of ornithurine birds, just proximal to the spine, there is a caudolaterally, or caudally, projecting tubercle for the insertion of *M. iliofibularis*, an important flexor of the tibiotarsus. The fibula is not well known for most non-ornithurine birds. In *Patagopteryx*, however, it is well-preserved and exhibits a robust tubercle for the *M. iliofibularis*, which projects directly laterally instead of caudolaterally or caudally (Chiappe, 1992a).

In velociraptorine theropods and other non-avian theropods, this tubercle (also known as the anterolateral process) typically projects cranio-laterally (Osborn, 1916; Lambe, 1917;

Ostrom, 1969; Osmólska et al., 1972; Welles, 1984; Currie & Zhao, 1993a).

*Mononykus* shares the condition of *Patagopteryx*, with a robust and laterally oriented *M. iliofibularis* tubercle (Fig. 18). Assuming that the anterolateral process of non-avian theropods and the tubercle for *M. iliofibularis* of ornithurines are homologous, this tubercle must have migrated caudally during the early evolution of birds. The lateral position of this tubercle in both *Mononykus* and *Patagopteryx* represents an 'intermediate' stage in this transformation.

4) Quadratojugal not contacting the squamosal (character 68). Neornithine birds are characteristic among theropods (and most archosaurs) in that the quadratojugal is a rod-like bone lacking a dorsal process for its articulation with the squamosal, which forms a free, ventrally projected zygomatic process. This derived condition is clearly present in Hesperornithiformes (Marsh, 1880; Bühler et al., 1988; Elzanowski, 1991). In *Patagopteryx* and Ichthyornithiformes the quadratojugal is not known (at least for the published specimens), but the presence of a zygomatic process indicates that the squamosal and the quadratojugal do not contact each other.

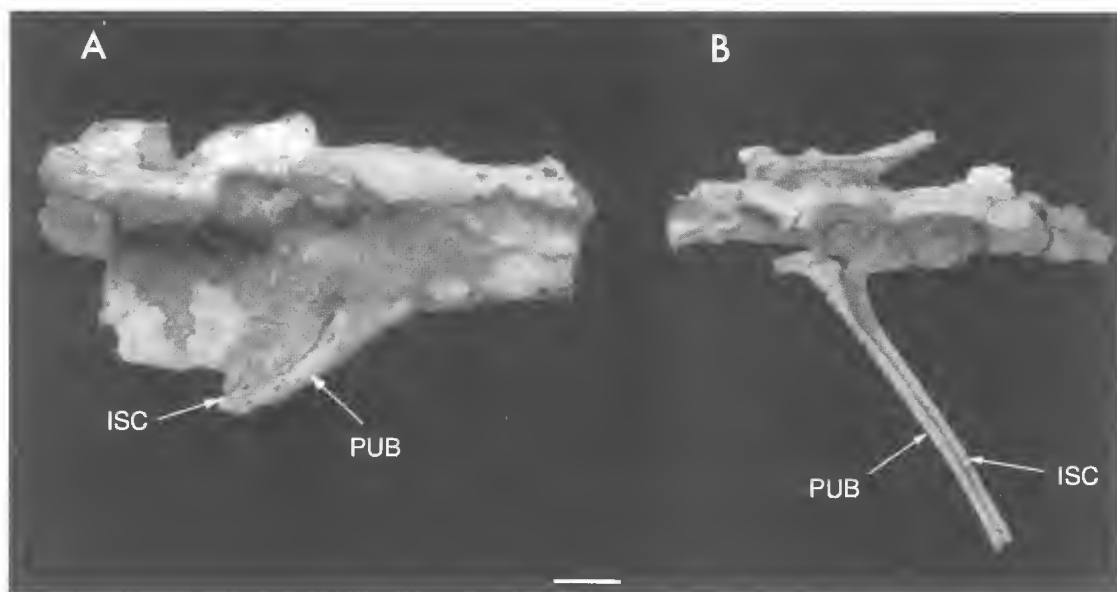


FIG. 17. Pelvis of *Mononykus* (MGI 100/975, left; MGI N 100/99, right) in lateral view. Note the subequal length of the pubis (PUB) and ischium (ISC). Scale = 1cm.

In *Archaeopteryx*, the quadratojugal has a dorsal process comparable to that of non-avian theropods, as it can be seen in the counter-slab of the recently found 'Solnhofen Aktien-Verein' specimen (Wellnhofer, 1993). The morphology of the squamosal of *Archaeopteryx* has been a matter of strong debate (cf. Wellnhofer, 1974; Whetstone, 1983; Bühler, 1985; Walker, 1985; Martin, 1991). In the 'Solnhofen Aktien-Verein' specimen, however, the squamosal appears to be well preserved and it shows a prominent ventral process (Elzanowski & Wellnhofer, 1995). Regardless the presence of these processes, it is not clear whether the quadratojugal and squamosal contacted each other, hence this character has been scored as uncertain for the Solnhofen bird.

In contrast to the condition present in neornithines, the squamosal of velociraptorines and all other non-avian theropods has an extensive contact with the quadratojugal (see Osborn, 1912; Colbert & Russell, 1969; Osmólska et al., 1972; Madsen, 1976; Weishampel et al., 1990; Currie & Zhao, 1993a; Clark et al., 1994). This relationship of the squamosal to the quadratojugal is in fact the primitive amniote condition (Romer, 1956).

In *Mononykus*, the quadratojugal forms a rod-like ossification, identical to the condition in neornithine birds, as it seen in the recently collected IGM 100/1001 from Ukhaa Tolgod (Dashzeveg et al., 1995). Furthermore, the squamosal

lacks any ventral projection. Clearly, these two bones do not contact each other.

5) Absence of medial fossa on the proximal end of the fibula (character 75). The medial surface of the fibula of neornithine birds is generally flat. This is the case in Hesperornithiformes and *Patagopteryx* (Chiappe, 1992a). As remarked above, the fibula is missing or poorly preserved in most non-ornithurine birds, and the present character is uncertain for Enantiornithes, *Iberomesornis* and *Archaeopteryx*.

In contrast, in *Deinonychus* the medial face of the proximal end of the fibula is excavated by a shallow fossa. This medial fossa is much more prominent in other non-avian theropods such as ornithomimids, tyrannosaurids (Lambe, 1917), *Sinraptor* (Currie & Zhao, 1993a) and *Allosaurus* (Madsen, 1976).

The proximal end of the fibula of *Mononykus* is flat in its medial surface, with no excavation (Fig. 18). A fragment of the fibula of *Patagonykus* shows that this derived morphology was also present in the Argentine taxon (Novas, this volume).

6) Absence of postorbital-jugal contact (character 95). The bird skull is characterised by having the orbit confluent with the archosaurian infratemporal fenestra (Zusi, 1993), a derived feature achieved by the reduction of the postorbital-jugal bar. This derived morphology is known to occur in Neornithes [although secondarily modified in some lineages (e.g., Psittaciformes,

Galliformes)], Ichthyornithiformes (Marsh, 1880) and Hesperornithiformes (Witmer & Martin, 1987; Bühler et al., 1988) in which the postorbital bone is absent. As with other cranial features, the presence or absence of a postorbital bone in *Archaeopteryx* is controversial. Wellnhofer (1974) regarded as a postorbital bone an impression on the counter-slab of the Eichstätt specimen, an identification followed by Walker (1985) who considered several fragments between the quadrate and the fronto-parietal suture as portions of the postorbital. Both Wellnhofer (1974) and Walker (1985) regarded the postorbital bone to contact the dorsocaudally projected caudal portion of the jugal, a feature well-preserved in the 'Solenhofer Aktien-Verein' specimen (Wellnhofer, 1993). Whetstone (1983), Bühler (1985) and Martin (1991), however, considered that a postorbital bone was absent in *Archaeopteryx*, and that this bone had no contact with the jugal bar caudally confining the orbit.

In velociraptorine theropods, as in all other nonavian theropods (Osborn, 1912; Colbert & Russell, 1969; Osmólska et al., 1972; Madsen, 1976; Weishampel et al., 1990), the jugal has a robust dorsal process that contacts a ventral process of the postorbital closing the orbit caudally.

*Mononykus* presents an intermediate condition between the morphology of non-avian theropods and that of more advanced birds such as Hesperornithiformes or Neornithes. In *Mononykus* (MGI 100/977) the postorbital has a long, slender ventral process, but this process does not reach the jugal. In fact, opposite the postorbital's ventral process, the jugal has a smooth, convex surface and no trace of a dorsal process is present. The orbit of *Mononykus* was clearly not closed caudally but connected with the infratemporal fenestra.

## DISCUSSION

This cladistic analysis supports the allocation of *Mononykus*, along with *Patagonykus* and *Alvarezsaurus*, within Aves (i.e., Avialae sensu Gauthier, 1986). This hypothesis is supported by four unequivocal synapomorphies of Aves

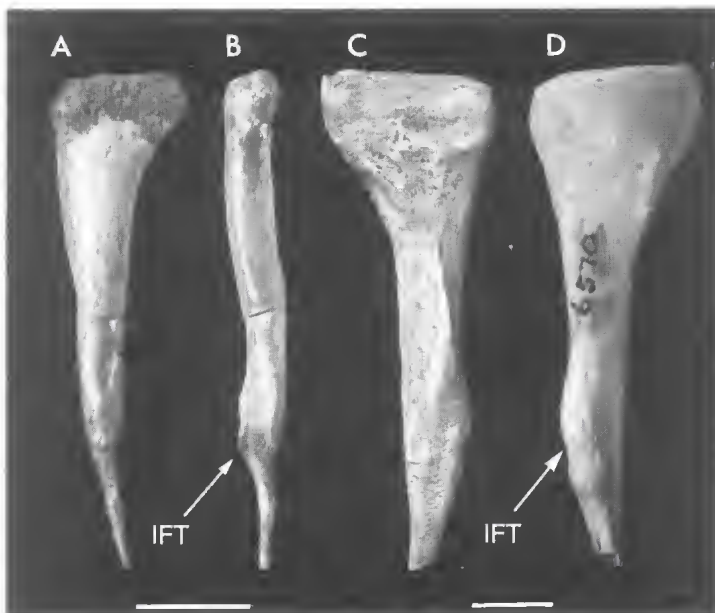


FIG. 18. Fibula of *Mononykus* (A, B, MGI N 100/99; C, D, AMNH-6570). A, D, lateral view; B, caudal view; C, medial view. IFT=tubercle for the *M. iliofibularis*. A, B, scale = 0.5cm; C, D, scale = 1.0cm.

present in *Mononykus* (character states 19a, 71, 81 & 85a) and six unequivocal synapomorphies (character states 13, 29, 30, 39, 44 & 69) supporting the monophyly of Metornithes (Perle et al., 1993), the clade composed of the common ancestor of *Mononykus* and Neornithes, plus all its descendants. The allocation of *Mononykus* within Aves is further supported by its possession of several other derived characters which diagnose, although equivocally, both Aves and Metornithes (character states 15, 46, 59a, 68, 74 & 95). The equivocal status of these synapomorphies means that pending determination of the condition in *Archaeopteryx*, these characters might become synapomorphies of either Aves or Metornithes. Although the precise status of these characters is yet unclear, they are both absent in the outgroup and symplesiomorphic of less inclusive clades (e.g., Ornithothoraces, Ornithurae), and examination of the data indicates that there is no optimisation dependence for these characters.

Our initial description of *Mononykus* (Perle et al., 1993), although brief, identified many of the characters diagnosing Metornithes presented in this paper. The avian affinity of *Mononykus* has been corroborated by Novas (this volume) on the basis of a cladistic analysis of a different data set, but criticised by others (Patterson, 1993; Feduc-



cia, 1994; Martin & Rinaldi, 1994; Ostrom, 1994; Wellnhofer, 1994).

As with any hypothesis, our hypothesis of relationship can be, and should be, tested by others. The rationale for cladistic analysis (described in detail by Farris, 1983 and Schoch, 1986) dictates that phylogenetic hypotheses are tested by the distribution of characters among taxa. Thus, to falsify our hypothesis: 1, characters supporting an alternative relationship for *Mononykus* must be identified; and 2, the weight of the evidence must support this alternative. Because the published criticisms do not furnish such evidence, our disagreements with these critics primarily concerns methodological issues and our criterion for evidence and testability in phylogenetic reconstruction.

Patterson's (1993) criticism was not focused on the phylogenetic position of *Mononykus*. Instead it reflects nomenclatural issues, which Norell et al. (1993b) subsequently addressed. Others centered their criticisms on the peculiar forelimb specialisations of *Mononykus*. For example, Wellnhofer (1994: 306) states that '*it would be very difficult to imagine how a primitive bird wing, such as that of Archaeopteryx, could have evolved into a forelimb like that of Mononykus*'. Such an assumption lacks rigor (Chiappe et al., 1995). If one agrees with Wellnhofer's argument it would be 'very difficult to imagine' how the flippers of a seal evolved from the forelimb of an ancestral carnivore. Likewise, Ostrom (1994) uses the flightless condition of *Mononykus* to claim that its keeled sternum must have evolved convergently, as a burrowing adaptation. Indeed, Ostrom misleadingly cites the keeled sternum as the only evidence we provide in support of our hypothesis, a claim belied by the figure from our original paper reproduced in his article, with five characters highlighted. The logic behind this argument seems to be that structures never change function, so that if similar structures have different functions they cannot be homologous. Thus, the explanation of this structure as an adaptation for burrowing takes precedence over the explanation of this structure as evidence for a close relationship between *Mononykus* and birds. The fallacy of such arguments has been pointed out many times (e.g., Gould & Vrba, 1982; Lauder, 1994, 1995). Function and structure are not always phylogenetically correlated (Lauder, 1995) and one wonders whether Ostrom would consider the forelimb of *Deinonychus* to be non-homologous with that of *Archaeopteryx* because they have different functions.

In their zeal to refute our phylogenetic hypothesis, some critics claim that the similarities we pointed out do not exist. For example, Feduccia (1994: 32) states '*the keeled breastbone doesn't resemble that of birds, but it is very much like that of a mole*'. While we do not deny that the stemum of *Mononykus* is similar to that of some moles, this similarity is irrelevant to comparisons between *Mononykus* and other maniraptoran archosaurs unless a close relationship between these archosaurs and this group of placental mammals is being seriously entertained. More to the point, the undeniable resemblance between the sternum of *Mononykus* and that of other birds cannot be ignored simply because it is at odds with a favorite scenario of bird evolution. Feduccia's other arguments against the avian affinities of *Mononykus* are mistaken or misleading. Within the context of his argument that birds are unrelated to dinosaurs, he claims that *Mononykus* '*has many typical theropod dinosaur features, including a large 'dinosaur' tail, a small head, and no collarbones*' (Feduccia, 1994: 32). The presence of many 'dinosaur' features in birds has been broadly documented (e.g., Ostrom, 1976a; Gauthier, 1986; Weishampel et al., 1990). Incidentally, none of these features are those pointed out by Feduccia. The presence of a '*large 'dinosaur' tail*' in *Mononykus* is erroneous, whereas the significance of the size of the head and the absence of clavicles (if not due to lack of preservation) is unclear. As noted above (character 19; see Characters Supporting the Monophyly of Aves, Character Analysis), the tail of *Mononykus* is like that of *Archaeopteryx* in being shorter than that of non-avian theropod dinosaurs. As for the lack of furcula, the presence of either unfused clavicles or furculae in several groups of theropod dinosaurs (see Barsbold, 1983; Bryant & Russell, 1993; Russell & Dong, 1993a) indicates that if they are indeed absent in *Mononykus* then this absence is a derived feature of this taxon. With regard to the skull, at the time our earlier paper was published the only evidence from the skull was a portion of a braincase and a bone tentatively identified as part of the maxilla. For these reasons our reconstruction of the skull was clearly indicated as such. We now know, from the recently discovered skull of specimen MGI 100/977, that the skull of *Mononykus* is actually larger than what we thought (Fig. 1). However, the suggestion that non-avian theropod dinosaurs have smaller skulls than birds is incorrect.

Martin & Rinaldi (1994) claimed that *Mononykus* is not avian but related to or-

nithomimid theropods (see also Martin, 1995). Unlike most of our critics, they at least proposed a specific hypothesis of relationships for *Mononykus*. Our differences with Martin & Rinaldi are both methodological and empirical. These authors both misunderstand and misrepresent cladistic techniques. In their view 'clearly almost any outcome is possible in that sort of an analysis [cladistic analysis]'. Martin & Rinaldi (1994) prefer to enumerate a series of characters that supposedly differentiates *Mononykus* from *Ichthyornis*, and which are alleged to be similarities between *Mononykus* and ornithomimids. Methodological differences aside, the problem with their procedure is that the majority of the characters listed for *Mononykus* are problematic or absent in this taxon. For example, Martin & Rinaldi claimed that *Mononykus* 'lacks or has few teeth', 'has a small head', 'no furcula', 'no free carpals', 'unusually short ribs', 'a long tail', 'astragalus enlarged to the point that the calcaneum is reduced to a nub or lost', and 'no antitrochanter on the pelvis'. As mentioned earlier, *Mononykus* has numerous tiny teeth and a skull which is larger than that illustrated in our original reconstruction, a tail shorter than any non-avian theropod, and a well-developed antitrochanter. The furcula (see above) and free carpals are not necessarily absent but not preserved in the known specimens. In fact, facets on the proximal articular surface of the carpo-metacarpus indicate that free carpals are missing (Perle et al., 1994).

Likewise, the astragalus and calcaneum of *Mononykus* are completely fused (Perle et al., 1994), preventing estimation of their relative sizes. The new specimen MGI 100/977 shows that the ribs are not particularly short. Obviously Martin & Rinaldi have based their comments on our original reconstruction (Perle et al., 1993: Fig. 2) despite the fact that the ribs were indicated (along with most of the skull) as unpreserved elements. The remaining characters used by Martin & Rinaldi (1994) are either primitive (e.g., elongated haemal arches, preacetabular ilium short), autapomorphic (e.g., ischium slender, reduced forelimbs, enlarged metacarpal I), or so highly variable as to be of uncertain generality (e.g., postacetabular ilium elongate, long neck). Of all the characters listed by Martin & Rinaldi, only the 'enlarged metacarpal I' (alular metacarpal in this paper) is derived and shared by ornithomimids. Nevertheless, the morphology of this metacarpal in *Mononykus* is distinctly different than that of ornithomimids. In or-

nithomimids, metacarpal I is more than half the length of metacarpals II and III (Barsbold & Osmólska, 1990); in advanced ornithomimids all the metacarpals are nearly equivalent in length (e.g., *Gallinimus*, *Ornithomimus*). Aside from length, however, all known ornithomimids have metacarpals that are proportionally similar. This is not true in *Mononykus* where the alular metacarpal (equivalent to metacarpal I) is significantly larger than the major and minor metacarpals (metacarpals II and III, respectively) (Fig. 14). This condition (an alular metacarpal that is larger than the remaining metacarpals) is synapomorphic of a group containing *Mononykus* and *Patagonykus*, and it is unrelated to the condition seen in ornithomimids. By rejecting our phylogenetic hypothesis, our critics have implicitly indicated that the evidence used to include *Mononykus* within Aves (in addition to the evidence presented here) is nonhomologous (i.e., homoplastic). These authors, however, have failed in providing logical support for such a claim. As extensively discussed elsewhere (e.g., Patterson, 1982; Rieppel, 1992, 1994; Pinna, 1991; Hall, 1994), homology is a two-statement concept ultimately based on the congruence of characters. Primary homology refers to statements about the similarity of characters prior to phylogenetic constructions, while secondary homology refers to interpretations of common origins through character congruence on a particular tree (Pinna, 1991); the largest number of characters which congruently support a specific hypothesis of relationships are considered as homologies. Therefore, a statement of nonhomology — as used by our critics — cannot be derived from a 'priori' observation, but it should be ultimately revealed by the mismatch between primary and secondary homology. In order to say, for example, that the carinate sternum or the absence of a jugal-postorbital contact shared by *Mononykus* and more advanced birds is not homologous, it is necessary to have an alternative hypothesis in which the 'congruence' between the distribution of characters supporting that hypothesis is maximised.

In using a cladogram to determine evolutionary relationships, one need only assume that the hierarchical distribution of characters reflects the evolutionary relationships of taxa. The possible function of a particular structure, or a scenario about how a particular structure or function arose are not relevant. Instead, the relationships identified by cladistic analysis are the ones that provide the framework for testing functional or

adaptational hypotheses (Coddington, 1988; Gatesy, 1995; Witmer, 1995) and to use these scenarios as evidence for or against a phylogenetic hypothesis confuses the phenomenon to be explained with the explanation for the phenomenon (Brady, 1985).

The avian affinity of *Mononykus* is supported by the present study and corroborated independently (Novas, this volume). Re-rooting this cladogram so that Alvarezsauridae falls outside Aves requires a number of additional steps. Four and six additional steps are required for the placing Alvarezsauridae either as the sister-group of Aves or the clade formed by Aves plus Velociraptorinae, respectively. As for any phylogenetic hypothesis, the addition of characters, taxa, or both to the data set may change the topology of the resultant cladogram. It is hoped that the discovery of more fossil taxa and better specimens (in particular representatives of the lineage leading to *Mononykus*, *Patagonykus* and *Alvarezsaurus*) will provide additional character information to further test this cladogram. Furthermore, an alternative outgroup hypothesis may modify our result. Several derived characters shared by *Mononykus* and other birds appear in some troodontid taxa but are absent in velociraptorines (e.g., characters 44 & 81). These similarities may suggest that troodontids are closer to birds than velociraptorines are; however this needs to be evaluated in light of a larger, more inclusive analysis. Our choice for velociraptorines instead of troodontids is based on the fact that the latter are poorly known and their selection as an outgroup would have added numerous missing entries to the data set.

### CONCLUSIONS

The cladistic analysis presented here supports the inclusion of *Mononykus* and the Alvarezsauridae, within Aves. The Alvarezsauridae is the sister-group of Ornithothoraces and is closer to Neornithes than is *Archaeopteryx*.

The alternative, that *Mononykus* is not a member of Aves, is based on misleading evolutionary assumptions and 'a priori' speculation. Falsification of our hypothesis requires that a new hypothesis better summarising the pattern of similarities shared by *Mononykus* and birds be proposed. Or, with the addition of new characters or taxa, our evidence for relationship (synapomorphy) is contradicted. What this means is that it is insufficient to authoritatively proclaim that *Mononykus* is not avian (or not a bird), without

proposing an alternative hypothesis of what it is related to (supported by character evidence).

Several years ago evolutionary biologists arrived at a consensus that hypotheses of phylogenetic relationships should be based on the simplest explanation for the distribution of characters shared among organisms. It is unfortunate that our critics support their claims with arguments that lie outside the lines of modern systematics and comparative biology.

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## APPENDIX 1

Skeletal characters and data-matrix used in the cladistic analysis. Multistate characters have been considered as additive except for characters 34, 40, 64, and 92 in which any two distinct states are separated by a single step. In the text and Fig. 2, 'a' and 'b' refer to states 1 and 2, respectively, of a multistate character. Scoring: 0 = primitive; 1, 2 = derived; ? = missing or uncertain.

1. Premaxillae in adults. *0*. unfused. *1*. fused.
2. Maxillary process of premaxillary. *0*. restricted to the rostral portion. *1*. forming most of the facial margin.
3. Frontal process of premaxilla. *0*. short. *1*. long, extending caudally to the level of lacrimals.
4. Premaxillary teeth. *0*. present. *1*. absent.
5. Osseous external naris. *0*. smaller, or *1*. considerably larger than antorbital fenestra.
6. Maxillary fenestrae. *0*. present. *1*. absent.
7. Rostral jugal border. *0*. away. *1*. very close to the caudal margin of the osseous external naris.
8. Ectopterygoid. *0*. present. *1*. absent.
9. Quadrate orbital process (pterygoid ramus). *0*. broad. *1*. sharp and point-shaped.

10. Quadratojugal. *0.* sutured to the quadrate. *1.* articulating in a cotyle in the lateral face of the quadrate mandibular process.
11. Quadrate pneumaticity. *0.* absent. *1.* present.
12. Articular pneumaticity. *0.* absent. *1.* present.
13. Prominent ventral processes on cervico-dorsal vertebrae. *0.* absent. *1.* present.
14. Dorsal vertebral count. *0.* 13-14. *1.* fewer than 13. *2.* fewer than 11.
15. Wide vertebral foramen in thoracic vertebrae, vertebral foramen/cranial articular facet ratio (vertical diameter) larger than 0.40. *0.* absent. *1.* present.
16. Synsacrum formed by *0.* less. *1.* more than 8 vertebrae.
17. Heterocoelous cervical vertebrae. *0.* absent. *1.* present.
18. Pygostyle. *0.* absent. *1.* present.
19. Caudal vertebral count. *0.* more than 35. *1.* fewer than 25-26. *2.* fewer than 15.
20. Ossified uncinat processes. *0.* absent. *1.* present.
21. Scapula and coracoid articulation. *0.* through a wide, sutured articulation. *1.* through more localised facets.
22. Procoracoid process. *0.* absent. *1.* present.
23. Coracoid shape. *0.* short. *1.* elongated with subrectangular profile. *2.* strut-like.
24. Scapulocoracoid articulation. *0.* at the shoulder (proximal) end of coracoid. *1.* well below to it.
25. Supracoracoid nerve foramen. *0.* centrally located. *1.* situated (often as an incision) in the medial margin of coracoid.
26. Coracoid and scapula. *0.* placed in the same plane. *1.* forming a sharp angle at the level of the glenoid cavity.
27. Scapular caudal end. *0.* blunt. *1.* sharp.
28. Scapular shaft. *0.* straight. *1.* sagittally curved.
29. Stemum. *0.* subquadrangular to transversally rectangular. *1.* longitudinally rectangular.
30. Ossified sternal keel. *0.* absent. *1.* present.
31. Proximal and distal humeral ends. *0.* twisted. *1.* expanded nearly in the same plane.
32. Ulna. *0.* shorter, *1.* longer or nearly equivalent to humerus.
33. Humeral head. *0.* concave cranially and convex caudally. *1.* globe shaped, craniocaudally convex.
34. Ventral tubercle of humerus. *0.* projected ventrally. *1.* proximally. *2.* or caudally, separated from the humeral head by a deep capital incision.
35. Humerus with well developed transverse ligamental groove. *0.* absent. *1.* present.
36. Humeral distal condyle location. *0.* mainly on distal aspect. *1.* cranial aspect.
37. Semilunate ridge on ulnar dorsal condyle. *0.* absent. *1.* present.
38. Ulnar shaft considerably thicker than radial shaft; radial shaft/ulnar shaft ratio. *0.* larger. *1.* smaller than 0.70.
39. Distal carpals and metacarpals. *0.* unfused. *1.* fused forming a carpometacarpus.
40. Extensor process on carpometacarpus. *0.* absent. *1.* round shaped. *2.* with a sharp point.
41. Pelvic elements. *0.* unfused. *1.* fused or partially fused.
42. Small acetabulum; acetabulum/ilium ratio equal or smaller than 0.11. *0.* absent. *1.* present.
43. Pubis more or less parallel to ilium and ischium. *0.* absent. *1.* present.
44. Prominent antitrochanter. *0.* absent. *1.* present.
45. Iliac fossa for *M. cuppedicus* (= *M. iliofemoralis internus*). *0.* present. *1.* absent.
46. Ischiadic terminal processes. *0.* in contact. *1.* lacking contact.
47. Pubic apex. *0.* in contact. *1.* lacking contact.
48. Pubis shaft laterally compressed throughout its length. *0.* absent. *1.* present.
49. Pubic foot. *0.* present. *1.* absent.
50. Femur with distinct fossa for capital ligament. *0.* absent. *1.* present.
51. Femoral anterior trochanter. *0.* nearly confluent with the greater trochanter. *1.* or fused to it forming the trochanteric crest.
52. Femur with prominent patellar groove. *0.* absent. *1.* present.
53. Femoral popliteal fossa distally bounded by a complete transverse ridge. *0.* absent. *1.* present.
54. Tibiofibular crest in the lateral condyle of femur. *0.* absent. *1.* poorly developed. *2.* prominent.
55. Femoral posterior trochanter. *0.* present. *1.* absent.
56. Tibia, calcaneum and astragalus. *0.* unfused or poorly coossified (sutures still visible). *1.* complete calcaneo-astragalar-tibial fusion.
57. Cranial cnemial crest on tibiotarsus. *0.* absent. *1.* present.
58. Extensor canal on tibiotarsus. *0.* absent. *1.* present.
59. Fibula with tubercle directed, for *M. iliofibularis*. *0.* anterolaterally. *1.* laterally. *2.* caudolaterally or caudally.



Taxalcharacters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36		
Velociraptorinae	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0		
Archaeopteryx	0	0	0	0	0	0	0	0	0	0	?	0	0	?	0	0	?	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	?	0	0	
Mononykus	0	0	0	0	0	?	0	?	0	0	?	?	1	?	1	0	0	0	1	?	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	
Alvarezsaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	0	0	?	0	0	0	?	0	?	?	?	?	?	?	?	?		
Patagonikus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	0	0	0	0	0	?	?	?	?	?	?	?	?	?	0	1	0	1
Iberomesornis	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	0	0	1	1	0	?	?	?	2	?	1	?	1	0	?	?	?	1	0	?	0	0	
Enantiornithes	1	0	1	0	1	?	?	1	0	?	?	0	1	?	1	1	1	1	?	0	1	0	2	1	1	1	1	0	1	1	0	1	0	2	1	1		
Patagopteryx	?	?	?	?	?	?	?	?	?	0	1	0	1	1	1	1	1	?	?	0	1	0	2	1	1	1	1	1	?	?	?	1	0	0	?	?	1	
Hesperornithiformes	1	1	1	1	1	1	1	1	1	1	0	1	1	2	1	1	1	1	2	1	1	1	2	1	1	1	1	1	1	1	0	1	0	0	?	?	1	
Ichthyornithiformes	1	?	1	?	?	?	?	?	1	1	1	1	1	2	1	1	0	1	?	?	1	1	2	1	1	1	1	1	1	1	1	1	1	1	2	1	1	
Neornithes	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	2	1	1	
Taxalcharacters	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69					
Velociraptorinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Archaeopteryx	0	0	0	0	0	0	0	0	0	?	0	0	0	?	0	0	?	0	0	0	0	0	?	0	0	0	?	0	0	0	0	0	0	0	0	?	?	0
Mononykus	0	0	1	0	1	0	0	1	1	1	1	1	1	0	1	0	0	0	1	0	0	0	1	0	0	0	1	1	0	?	0	1	0	0	0	1	1	
Alvarezsaurus	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	0	0	?	?	0	?	?	?	?	?	?	
Patagonikus	0	0	1	0	0	?	?	0	1	1	?	1	1	0	?	0	0	0	1	0	0	0	1	0	0	0	?	0	0	?	?	0	0	?	?	?		
Iberomesornis	?	1	?	?	?	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	0	0	?	0	0	0	?	?	?	
Enantiornithes	1	1	1	1	1	0	?	1	0	1	0	0	0	1	1	0	1	1	1	0	1	0	1	0	0	?	1	0	1	1	0	0	0	1	?	1		
Patagopteryx	?	1	1	?	1	0	0	1	1	1	1	0	1	?	?	0	1	2	1	1	0	0	1	1	0	0	1	1	1	1	0	0	1	0	1	1		
Hesperornithiformes	?	1	?	?	?	1	1	1	1	1	1	1	1	?	?	1	?	1	1	1	1	1	2	1	1	1	1	1	1	2	1	1	1	1	1	1		
Ichthyornithiformes	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	2	1	1	1	1	1	1	1	2	1	1	1	1	1	1		
Neornithes	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
Taxalcharacters	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99								
Velociraptorinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Archaeopteryx	0	1	1	0	?	0	0	?	0	0	0	1	0	?	?	1	1	1	1	0	?	0	?	0	0	0	?	0	0	0	0	0	0	0	0	0		
Mononykus	0	1	0	0	1	1	1	1	1	1	1	?	?	?	1	1	0	?	?	?	?	1	1	?	1	0	0	1	?	0	?	?	?	?	?	?		
Alvarezsaurus	?	?	0	0	?	?	0	0	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
Patagonikus	?	?	0	?	?	?	1	1	1	1	1	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
Iberomesornis	?	?	?	0	?	0	0	0	0	?	?	?	?	?	?	1	?	1	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
Enantiornithes	1	1	1	1	1	0	1	0	0	0	0	?	0	1	1	1	1	1	?	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0
Patagopteryx	?	?	0	1	1	0	1	0	1	0	0	?	1	1	1	2	1	0	?	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Hesperornithiformes	0	1	1	1	1	0	0	0	0	0	?	1	1	1	2	0	0	1	0	1	?	1	1	1	1	1	1	0	1	0	1	0	1	0	1	0	1	
Ichthyornithiformes	?	?	1	1	1	?	0	?	0	0	0	?	?	?	?	1	1	1	?	?	0	1	1	0	1	?	?	?	?	?	?	?	?	?	?	?	0	1
Neornithes	1	?	1	1	1	0	0	0	0	0	0	1	1	1	1	2	1	1	1	0	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	

Character data matrix.

60. Fibular articulation. *0*. with the calcaneum. *1*. greatly reduced distally, without articulation with the calcaneum.

61. Metatarsals II-IV completely fused one to each other. *0*. absent. *1*. present.

62. Distal tarsals. *0*. free. *1*. completely fused to the metatarsals.

63. Metatarsal V. *0*. present. *1*. absent.

64. Proximal end of metatarsal III. *0*. in the same plane as metatarsals II & IV. *1*. reduced, not reaching the tarsals (arctometatarsalian condition). *2*. plantarily displaced with respect metatarsals II & IV.

65. Well developed tarsometatarsal intercondylar eminence. *0*. absent. *1*. present.

66. Tarsometatarsal distal vascular foramen. *0*. absent. *1*. present.

67. Iliac brevis fossa. *0*. present. *1*. absent.

68. Quadratojugal-squamosal contact. *0*. present. *1*. absent.

69. Ischium. *0*. less than two-thirds. *1*. two-thirds or more of pubis length.

70. Lateral processes on the sternum. *0*. absent. *1*. present.

71. Teeth (adult). *0*. with serrated crowns. *1*. unserrated crowns.

72. Supracetabular lip. *0*. present. *1*. absent.

73. Cervical ribs. *0*. articulated with vertebrae. *1*. fused to vertebrae forming the costal processes.

74. Proximal end of fibula. *0*. excavated by a medial fossa. *1*. nearly flat.

75. Hypertrophied olecranon process. *0*. absent. *1*. present.

76. Synsacrum procoelous. *0*. absent. *1*. present.

77. Caudal portion of the synsacrum forming a prominent ventral keel. *0*. absent. *1*. present.

78. Caudal articular surface of synsacrum convex. *0*. absent. *1*. present.

79. Humerus. *0*. with two distal condyles. *1*. single condyle.

80. Prominent ventral projection of the lateroproximal margin of the proximal phalanx of digit I. *0*. absent. *1*. present.

81. Caudal tympanic recess. *0*. opens on the rostral margin of the paraoccipital process. *1*. opens into the collumelar recess.

82. Quadrate. *0*. with two distal condyles. *1*. with three condyles forming a triangle.

83. Basicranial fontanelle on the ventral surface of the basisphenoid. *0.* present. *1.* absent.
84. Hyposphene-hypantrum accessory intervertebral articulations in trunk vertebrae. *0.* present. *1.* absent.
85. Distal caudal prezygapophyses. *0.* elongate. *1.* short *2.* absent.
86. Prominent acromion in the scapula. *0.* absent. *1.* present.
87. Completely reverted hallux (arch of unguual phalanx of digit I opposing the arch of the unguuals of digits II-IV). *0.* absent. *1.* present.
88. Caudal maxillary sinus. *0.* absent. *1.* present.
89. Procoelous caudals. *0.* absent. *1.* present.
90. Carotid processes in intermediate cervicals. *0.* absent. *1.* present.
91. Ungual phalanx on major digit (digit II). *0.* present. *1.* absent.
92. Dentary teeth. *0.* set in sockets. *1.* set in a groove *2.* absent.
93. Postorbital. *0.* present *1.* absent.
94. Fossa for the femoral origin of *M. tibialis cranialis*. *0.* absent. *1.* present.
95. Postorbital-jugal contact. *0.* present. *1.* absent.
96. Subequal cotyla of ulna. *0.* present. *1.* absent.
97. Costal facets in sternum. *0.* absent. *1.* present.
98. Bony mandibular symphysis. *0.* absent. *1.* present.
99. Proximal phalanx of manal major digit (digit II). *0.* of normal shape. *1.* flat and craniocaudally expanded.